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Did the thylacine violate the costs of carnivory? Body mass and sexual dimorphism of an iconic Australian marsupial

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Revised submission:	28 July 2020
Final acceptance:	28 July 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-1537.R0 (Original submission)

Review form: Reviewer 1 (Jack Ashby)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
This represents an important addition to the field, with a clear conclusion to a previously debated topic. Suggested revisions are attached. (See Appendix A)

Review form: Reviewer 2 (Darin Croft)

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is a well-crafted manuscript, and I enjoyed reading it. My comments are included in the attached file. (See Appendix B)

Decision letter (RSPB-2020-1537.R0)

22-Jul-2020

Dear Mr Rovinsky

I am pleased to inform you that your manuscript RSPB-2020-1537 entitled "Did the thylacine violate the costs of carnivory? Body mass and sexual dimorphism of an iconic Australian marsupial." has been accepted for publication in Proceedings B. Congratulations!!

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

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When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as ‘tracked changes’ to be included in the ‘response to referees’ document.

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2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr John Hutchinson
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Dear Authors,

Thank you for your submission to Proceedings B. Your paper has now been seen by two reviewers, and based on their recommendations I believe your paper will be suitable for acceptance pending minor revisions.

Both referees were generally happy with your manuscript as it stands, yet they provide helpful comments which I believe will improve the contextualisation and reach of your manuscript. For example, I believe Reviewer 2's recommendation to include more discussion about potential metabolic differences between marsupials and placentals will be very useful, as is their suggestion to provide additional information on potential implications of this work for constraining aspects of the palaeobiology of extinct South American metatherian carnivores. Beyond these points, the referees provide a number of additional helpful suggestions that I hope you will take under consideration as you prepare a revised version of your manuscript.

Congratulations on a very interesting manuscript—I look forward to seeing a revised draft.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
This represents an important addition to the field, with a clear conclusion to a previously debated topic. Suggested revisions are attached.

Referee: 2

Comments to the Author(s)
This is a well-crafted manuscript, and I enjoyed reading it. My comments are included in the attached file.

Author's Response to Decision Letter for (RSPB-2020-1537.R0)

See Appendix C.

Decision letter (RSPB-2020-1537.R1)

28-Jul-2020

Dear Mr Rovinsky

I am pleased to inform you that your manuscript entitled "Did the thylacine violate the costs of carnivory? Body mass and sexual dimorphism of an iconic Australian marsupial." has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

This paper sets out to estimate body mass for thylacines from museum specimens, in order to test the validity of previous conclusions that their morphology suggested that they preyed on animals smaller than themselves, but their reported body mass indicated that they were in a guild that preyed on larger animals. The authors found previous mass estimates to be too high, and their revised estimates, achieved from specimen measurements tested against volumetric analysis, mean that the thylacine's size fits assumptions that it fed on smaller animals (but could take larger prey if needed).

They also establish criteria for assigning sex to thylacine specimens of previously unknown sex. These could be more clearly articulated in order to make it easy for museum staff to sex their specimens – which in turn could increase their value for future research.

This represents an important contribution to the literature. The paper sets out the question to be answered, and then answers it. In so doing the authors resolve a previously problematic aspect of our understanding of the biology of an icon of global extinction.

3D scan data for thylacine skeletons are in demand both in science and entertainment, so the creation of these also adds value.

Below are a few minor revisions, with some additional conclusions that could be drawn.

L24 – worded in such a way that it's potentially unclear if the masses given represent the prior estimates or their new findings.

L25 – used 14.5kg as the lower end of the range, while L36 uses 14kg.

S2 – reference to Chapter 3, Table A3.5 and Table A.3.8 (in "Note on S2"), although there is no Chapter 3. (also Chapter 3 in the table in S14)

L57 – costs not cost

L83 – should be NRM 566599 (not NRM A56 6599)

S6 – Is one of the column headers missing some text ("Volumetric model // low weight // low")?

S7 – figure misses PL on diagram

S7 – table legend includes "UMZN" – should be "UMZC"

L188 – do you mean post hoc, rather than ad hoc?

L200 – it would increase readability if authors explicitly stated here that previous models had concluded that morphologically thylacines were adapted to prey smaller than themselves (as in e.g. their ref 17), despite the larger body size estimate.

L207 / fig 2d – not convinced the figure is made sufficient use of (or actually adds any value in its current form). The text implies the position of the coyote/wolf can be interpreted from the figure, but they cannot. Needs more interpretation to justify inclusion of the figure.

L212-214 – this point could be made in simpler terms. It's also apparently contradictory with L211, where the authors state there is no sex-based allometric trend. I am left confused what caused the inference that there were two types of thylacine.

L232 – missing word "tentatively *estimate* mass"

L242 – it would be instructive to restate the male and female mass estimates they produced; to clearly articulate how to sex a thylacine.

L243-234 – value would be added by stating the ranges in which a specimen of unknown sex could be assigned as male or female based on mass and cranial size.

- Another conclusion is that their estimate average weight for female thylacines is similar to the upper weight range of a devil (which occasionally reach 13kg), with potential implications for the relative roles of each of these carnivores in Australian environments, and interactions between them.

- a useful historical addition would be to mention that this further suggests that thylacines were not likely to have been major predator on sheep – an accusation which brought about the bounty which led them to extinction.

- value would be added by explicitly stating in the body of the paper the upper range of estimated size found by their estimates (i.e. which specimen is the biggest?)

Appendix B

This is an intriguing and very useful analysis that fits well within the scope of Proceedings of the Royal Society B. Overall, I think it is well-executed, and I have no major criticisms of the data, methods, analyses, or interpretations. The authors bring a great deal of data to bear on the question of the body mass of the thylacine and support their analyses with detailed supplementary data. I don't think there is anything major about the manuscript that must be modified, but I do have a a few suggestions the authors may wish to consider.

The question of whether the thylacine violated the costs of carnivory is a good "hook" and a logical application of these new body mass estimates. However, the costs of carnivory are based on energy budgets, and the cited studies of Carbone et al. (1997, 2007) focus exclusively on placental carnivorans. Are the costs the same for marsupial carnivores, given differences in metabolic rates between marsupials and placentals? My sense is that such difference wouldn't have a major effect on energy budgets, if any, and the data presented in Fig. 2d seem to indicate that marsupials are not outliers relative to placentals, but I think this issue is something that should be mentioned and/or discussed. I suspect most readers are familiar with the differences in metabolic rates between marsupials and placentals and will be left wondering about this if it isn't addressed directly in the manuscript.

In addition, I think the authors are missing an opportunity to discuss their study in a broader context and provide relevance to researchers outside of Australia. South America was home to a large diversity of carnivorous metatherians that have no living descendants or close relatives (sparassodonts), and many studies have focused on the paleobiology of these taxa. For comparative data, these studies have relied on extant Australian marsupial carnivores (including the recently-extinct thylacine) in addition to carnivorans, particularly in terms of estimating body mass and diet. It would be useful to discuss the implications of this study for estimating BM in sparassodonts (e.g., could molar row length also be over-estimating BM in these species?) as well as implications for prey selection (e.g., relative to the conclusions of Ercoli et al. 2014). Croft et al. (2018) present a recent analysis of diversity patterns in this group, and Prevosti and Forasiepi (2018) includes a review of the group.

Finally, beyond carnivores and marsupials, I think this study has important implications for estimating body mass in extinct mammals in general, particularly extinct groups with no living descendants or close relatives (or, at least, closely similar relatives). The recent review of Croft et al. (2020) discusses this issue in relation to the extinct "ungulates" of South America and advocates using head-body length and similar variables for BM estimates rather than dental measurements. Millien and Bovy (2010) discuss this in giant caviomorph rodents of South America. The present study provides another example of how using dental measurements can result in over-estimates of BM and could advocate for using volumetric and other methods for extinct taxa, when possible. It also illustrates how using a more accurate but less broadly-applicable method (volumetric renderings) can be used to assess the accuracy of methods that require less complete material and are more easily applied to fossils (long bone circumferences). Hopkins (2018) provides a good review of estimating BM in extinct taxa in general that would probably be more relevant to cite than some of the carnivore-focused references cited in lines 51-2. Damuth (1990) is also quite relevant.

I found it a little strange that the authors do not seem to consider differences in size between the sexes as sexual dimorphism. For example, Section a of the results discusses this size dimorphism, but Section b is titled "Sexual dimorphism" and even starts with this sentence:

“The sexes are significantly different in size across all metrics.” Maybe this just comes down to being clearer about size versus shape, but I think most readers would think of size as the most obvious form of sexual dimorphism rather than something that is separate from it.

I like the figures, but the font size of the text is very small in some parts and makes it difficult to appreciate the information that is presented. Figure 2a is really interesting from the standpoint of predicting body mass, but I think it gets a little lost because so much information is crammed into a small space. It makes sense having figs. 2b and 2c close to one another, but I also think 2c would fit well in Figure 3, which deals with dimorphism. I think 2d could be separate, since it focuses on predators vs. prey rather than just thylacine data. I know there are constraints on the number of figures, particularly relative to text length, and I’m not sure of the best resolution, but I would do some more thinking about how to best portray the data in the figures and whether anything could be moved to supplementary data if need be. Since sexual dimorphism isn’t the main thrust of the paper, some/all of Figure 3 could be moved to supplementary data if space is a constraint.

<u>References Cited:</u>

Croft, D. A., J. N. Gelfo, and G. M. López. 2020. Splendid innovation: The South American native ungulates. Annual Review of Earth and Planetary Sciences 48:249-290.

Croft, D. A., R. K. Engelman, T. Dolgushina, and G. Wesley. 2018. Diversity and disparity of sparassodonts (Metatheria) reveal non-analogue nature of ancient South American mammalian carnivore guilds. Proceedings of the Royal Society B: Biological Sciences 285:20172012.

Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements; pp. 229-253 *in* J. Damuth, and B. J. MacFadden (eds.), Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge University Press, Cambridge, United Kingdom.

Ercoli, M. D., F. J. Prevosti, and A. M. Forasiepi. 2014. The structure of the mammalian predator guild in the Santa Cruz Formation (late early Miocene). Journal of Mammalian Evolution 21:369-381.

Hopkins, S. S. B. 2018. Estimation of body size in fossil mammals; pp. 7-22 *in* D. A. Croft, D. F. Su, and S. W. Simpson (eds.), Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities. Springer Nature, Cham, Switzerland.

Millien, V., and H. Bovy. 2010. When teeth and bones disagree: body mass estimation of a giant extinct rodent. Journal of Mammalogy 91:11-18.

Prevosti, F. J., and A. M. Forasiepi. 2018. Evolution of South American mammalian predators during the Cenozoic: paleobiogeographic and paleoenvironmental contingencies. Springer Geology, Cham, Switzerland, 186 pp.

Appendix C

Reviewer 1 Comments	Author Response	Change in Text
L24 – worded in such a way that it's potentially unclear if the masses given represent the prior estimates or their new findings.	Yes – thank you for the catch, and you are correct. The text has been revised to clarify.	We demonstrate that prior estimates substantially overestimated average adult thylacine body mass. We show mixed-sex population mean (16.7 kg), mean male (19.7 kg), and mean female (13.7 kg) body masses well below prior estimates, and below the 21 kg costs of carnivory threshold.
L188 – do you mean post hoc, rather than ad hoc?	yes! - changed	
L200 – it would increase readability if authors explicitly stated here that previous models had concluded that morphologically thylacines were adapted to prey smaller than themselves (as in e.g. their ref 17), despite the larger body size estimate.		Previous mass estimates had placed the thylacine well over the 21.0 kg costs of carnivory threshold, suggesting a predation strategy focusing on large-bodied prey around or above the size of the predator. This feeding ecology conflicts with functional studies suggesting that the thylacine was poorly adapted to handle large-bodied prey.
L207 / fig 2d – not convinced the figure is made sufficient use of (or actually adds any value in its current form). The text implies the position of the coyote/wolf can be interpreted from the figure, but they cannot. Needs more interpretation to justify inclusion of the figure.	These additions to the figure (now Figure 3) have been made, as well as more tie-in with the paper. Hopefully this satisfies the concern – thank you for the suggestion, it was needed.	

L212-214 – this point could be made in simpler terms. It's also apparently contradictory with L211, where the authors state there is no sex-based allometric trend. I am left confused what caused the inference that there were two types of thylacine.	Agreed – the wording was unhelpfully vague. Hopefully, the revision clears the mud a little, although there is nothing but unhelpfully vague commentary regarding the two 'types' of thylacine. You do still see it crop up in pop literature now and again, so thought it best to address it as best as possible here. Regarding the "contradictory" issue – again that was due to vague and unhelpful writing on our part. There is no significant difference in shape that is not explained by allometry – it mostly seems to be size-based.	While we do find evidence of positive allometry in the cranium in both sexes, especially in rostral and facial width, we find no evidence of differing allometric trajectories or non-allometric difference in shape between the sexes. This also suggests that the two 'kinds' or 'types' of thylacine sometimes noted in the literature, a short-nosed 'bull-dog' thylacine, and a 'greyhound' thylacine (49-52), were simply observations of the strong size dimorphism coupled with the positive allometric trends in cranial measurements, as postulated by Allport (50) and Moeller (51).
L242 – it would be instructive to restate the male and female mass estimates they produced; to clearly articulate how to sex a thylacine.	Thanks for the suggestion; this has been added.	The strongly sexually size dimorphic thylacine (female mean: 13.7 kg; male mean: 16.7 kg) instead occupied the 14.5—21 kg threshold characterised by small-prey predators that are capable of switching to relatively large-bodied prey if the situation presents itself.
L243-234 – value would be added by stating the ranges in which a specimen of unknown sex could be assigned as male or female based on mass and cranial size.	Agreed; these ranges have been added	Relatively confident sex assignment of thylacines is possible based on mass (female: < 14.8 kg; male > 16.7 kg) and cranial size via linear metric CVA (but a rough simple metric is: female CBL < 203 mm; male CBL > 214 mm), and we post hoc sexed an additional 23 specimens.

- Another conclusion is that their estimate average weight for female thylacines is similar to the upper weight range of a devil (which occasionally reach 13kg), with potential implications for the relative roles of each of these carnivores in Australian environments, and interactions between them.	A small section pointing this overlap out has been added. Regarding potential interactions – with no reliable ecological data on the thylacine it is difficult to make reasonable conjecture as to interactions. I'd expect it would be similar to what is already suspected – devils continue to scavenge – which is unlikely to have been a large part of the thylacine's repertoire, and devils still potentially dominate access to carcasses over the other carnivores.	The mass of the female thylacine (mean 13.7 kg) overlaps with that of large Tasmanian devil (Sarcophilus harrisii) males, which average ~8.8 kg and occasionally reach weights of > 12 kg (48; Jones 2008; Andersen et al 2020). A similar overlap in mass is observed between the sympatric eastern quolls (Dasyurus viverrinus) and female spotted-tailed quolls (Dasyurus maculatus), and between male D. maculatus and female S. harrisii (Jones 1997; Jones & Barmuta 1998). This overlap is not seen in other functional characters, such as canine strength or temporalis muscle area, between the quolls and devils (Jones 1997). Substantial overlap in these characters has been noted between Tasmanian devils and thylacines, with female thylacines having substantially weaker canines than devils of both sexes, and a smaller area for the temporalis than male devils (Jones, 1997). While there is no reliable data for the feeding ecology of the thylacine, it may be that this overlap in mass and functional characters prompted niche separation in areas of sympatry, or that the mass overlap potentially allowed devils to dominate carcass access and utilisation over the entire range of marsupial carnivores.

- a useful historical addition would be to mention that this further suggests that thylacines were not likely to have been major predator on sheep – an accusation which brought about the bounty which led them to extinction.	We think this is very probable – at least, predation of adult sheep is likely to have been highly unlikely. But… even "small" predators such as culpeo and red fox often take infant and juvenile sheep, so we feel that would require either more/different data or an unnecessary amount of parsing of the language to adequately address. Additionally, we don't necessarily want to wade into what may amount to a sociocultural minefield regarding that aspect with this particular paper – we've encountered quite a lot of heated opinions on the subject and feel that would be better served by a more pointed study. Do we agree with you? Yes. Do we think we want to get "into that" with this paper… not necessarily.	
- value would be added by explicitly stating in the body of the paper the upper range of estimated size found by their estimates (i.e. which specimen is the biggest?)	Maximal mass range across the corrected equations (cLMRL, cUMRL, cCBL) have been added)	The total range estimate across all three corrected equations indicates a potential minimum adult size of 9.8 kg (NMV C 5750.1, female) and a maximum of 28.1 kg (LEEDM C.1869.46.2.4088; sex unknown).

Reviewer 2 Comments	Author Response	Change in Text
Are the costs the same for marsupial carnivores, given differences in metabolic rates between marsupials and placentals?	This is an excellent question, and I don't know if it can be adequately answered with the paucity of extant larger-bodied marsupial predators (in that they no longer exist!). Studies have suggested that the trend found in Carbone et al. (2007) should be similar if not the same within marsupials (e.g., Riek & Bruggeman, 2013) – whether or not the specific elevation of that regression is the same is another story. And you are correct – the marsupial data we do have suggest that marsupials "play by the same rules", so I think it safe to say that the thylacine wouldn't violate the costs either way. There has been addendums added to the Introduction and Discussion sections for this. Riek, A. & Bruggeman, J. (2013) Estimating field metabolic rates for Australian marsupials using phylogeny. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 164, 598-604.	

I think the authors are missing an opportunity to discuss their study in a broader context and provide relevance to researchers outside of Australia…	This is a good point – indeed, we are just another stone set in the house of "be careful with those regressions, Eugene", aren't we? We have added discussion relating to this and the broader implications (hopefully) without overstepping our bounds.	The poor accuracy of the dental regressions in mass estimation across dissimilar morphologies or magnitudes of size (e.g., extrapolating from the relatively short-faced, ~3 kg D. maculatus to the relatively long-faced, much larger T. cynocephalus) has implications beyond reconstructing the body mass of Thylacinus. Dental regressions have been widely used to reconstruct the mass of extinct marsupials (61-65), non-marsupial metatherian sparassodonts (66-71), and stem metatherians (72). Many of these taxa are well within the sizes and/or morphologies included in the base data of the regressions, though many – such as the sparassodonts – are not. Overestimations of mass for these taxa could affect interpretations of metatherian ecology, competition, and extinction (67, 70, 73, 74) as all of these are strongly affected by body mass. These results highlight the general difficulties in extrapolating body mass for species with no close living relatives, or with living relatives that are drastically different in shape or size (22, 30, 60, 75-80). The advantages of using 'conventional' (linear metric-based regression) techniques – their simplicity, objectivity, and applicability to often-incomplete fossil remains – should not be ignored. However, their associated caveats and potential drawbacks also need to be kept in mind, particularly when applying them to wildly disparate taxa (30, 31, 80, 81). Where possible, it may be highly beneficial to use

		multiple methods, including those (such as volumetric methods, GDI, etc.) that are not constrained to single-element regressions, to provide a method of cross-validation and to avoid the ‘one bone effect’ often seen in such estimations.

I found it a little strange that the authors do not seem to consider differences in size between the sexes as sexual dimorphism.	I think maybe this has just been misunderstood? We are careful to separate these two aspects of sexual dimorphism – size and shape. As you stated, dimorphism in size is indeed the most obvious example of sexual dimorphism (and could probably be considered the 'classic' metric). But, there can also be non-size-related differences in shape (sexual shape dimorphism), as examined in Blagojević & Milošević-Zlatanović (2011), Morris & Carrier (2016), and Schwarzkopf (2005) for a brief grab-bag of examples across varying clades. Since the thylacine had been noted to have two distinct 'types', we thought it prudent to test for both size and shape dimorphism – it would also have been interesting to see if there were any differences in shape between the sexes that were not attributable to size alone, to explore any social signalling, feeding niche, behavioural, etc. differences that might manifest in the skull shape. Our results –do- show strong sexual size dimorphism, but no difference in shape between the sexes that is distinct from the common allometric trends in the linear metrics or 3D shape variables. Blagojević, M. & Milošević-Zlatanović, S. (2011) Sexual shape dimorphism in Serbian roe deer (*Capreolus capreolus* L.). Mammalian Biology, 76, 735-740.	

	Morris, J.S. & Carrier, D.R. (2016) Sexual selection on skeletal shape in Carnivora. Evolution, 70, 767-780. Schwarzkopf, L. (2005) Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*). Herpetologica, 61, 116-123.	
I like the figures, but…	Thank you for the feedback – figures (and text therein) have been adjusted to hopefully fix the issues	